Effects of Water Stress and Drought Hardening on Photosynthesis, Stomatal Conductance, and Osmotic Potential of *Populus deltoides* Clones

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INTRODUCTION

Net photosynthetic rate is known to decline with increased water stress in poplars (Regehr et al. 1975, Scarascia–Mugnozza et al. 1986). Some of the effects of water stress on photosynthesis are due to closure of stomata, reduction in leaf area, and decrease in the efficiency of carbon fixation (Kramer 1983). Despite a close relationship reported between photosynthetic rate and stomatal conductance, factors other than CO_2 diffusion also affect photosynthesis (Scarascia–Mugnozza et al. 1986). According to Scarascia–Mugnozza et al. (1986), leaf conductance accounted for about 40% of the reduction in photosynthetic rate in Populus deltoides Bartr. as dehydration increased. Regehr et al. (1975) reported that maximum photosynthesis in P. deltoides remained unchanged as leaf water potential (Ψ_w) decreased toward –0.8 MPa. The rate then dropped sharply to almost zero at –1.0 to –1.1 MPa. They found that maximum photosynthesis did not coincide with peak stomatal conductance, suggesting that factors other than CO_2 availability influenced photosynthesis.

Davies and Kozlowski (1977) used a ratio of photosynthesis to leaf conductance as an indication of direct effects of water stress on photosynthesis, i.e. effects independent of stomatal closure. They suggested that plants that show delayed stomatal opening following rewatering after a drought period might compete successfully on drier sites. According to Hutmacher and Krieg (1983), cotton (Gossypium hirsutum L.) plants subjected to slowly developing water stress showed

greater reductions in photosynthesis than in leaf conductance, indicating non–stomatal limitations of photosynthesis.

Kelliher and Tauer (1980) suggested using leaf conductance as an important criterion in selecting drought resistant clones of P. deltoides. However, Tschaplinski and Blake (1989a) reported that using stomatal conductance, transpiration rate, and xylem pressure potential as selection criteria in hybrid poplars is not effective because of the different mechanisms of drought resistance employed by different clones.

Ackerson and Hebert (1981) reported that non–stomatal factors severely limited photosynthesis at high leaf water potential in cotton plants that were adapted (pre–stressed). However, under dry conditions, adapted plants maintained photosynthesis to a much lower Ψ_w than non–adapted control plants. The maintenance of continued photosynthesis at low Ψ_w in adapted plants was due to osmotic adjustment (Ackerson and Hebert 1981, Ackerson 1981). Osmotic adjustment, which has been found to occur in several P. deltoides clones exposed to a series of dry cycles (Tschaplinski and Blake 1989b), enables cell enlargement and growth to continue at water potentials that would otherwise be inhibitory. It also helps keep stomata open and the photosynthetic apparatus operating at lower Ψ_w than if there was no osmotic adjustment (Kramer 1983). Since water stress is reported to cause cellular damage (Giles et al. 1976), accumulation of certain osmotica such as sugars may also help stabilize membrane structures (Santarius 1973, Hoekstra et al. 1989). The role of osmotic adjustment in photosynthesis may thus be more than maintenance of the stomatal turgor.

The purpose of this study was 1) to determine the existence and extent of osmotic adjustment in two P. deltoides clones, 2) to determine net photosynthetic rate and stomatal conductance of these clones at different levels of water stress, and 3) to determine the effect of drought hardening on changes in P. deltoides leaf water potential, photosynthetic rate, and stomatal conductance during a stress period.

MATERIALS AND METHODS

Forty cuttings each of two clones of eastern cottonwood (Ohio Red, No. 217–1 and Platte, No. 36–5, Ying and Bagley 1976, Coleman 1982) were planted in a greenhouse on May 16, 1990, in 15 L containers with a mixture of silty–clay–loam soil, perlite, vermiculite, and peat (1:1:1:1 by volume). The two clones were selected based on differences in their water relations and similarity in drought hardening responses in a field study (Gebre 1989). To each container 35 g of slow release fertilizer was added (Osmocote 19–6–12, N–P–K). The temperature in the greenhouse was approximately 24°C/16°C. Supplemental illumination of 16 µmol m^{-2} s^{-1} extended the photoperiod to 16 hours. Plants were all watered daily until the experiment started on August 28, 1990. Plants of similar sizes were then divided into three treatments each of 5 plants per clone. One group was watered daily (control), a second group was watered every 3rd day (TRT 1), and a third group watered every 4th day (TRT 2). Extra plants (about 20) were also watered daily. One day before sampling, the leaf with plastochron index (LPI) of 8 was marked on each plant. LPI was approximated by numbering leaves

basipetally from the index leaf, the first leaf with a lamina length was equal to or greater than 2.0 cm (Tschaplinski and Blake 1989a).

Plants were sampled before and after rewatering, after being subjected to 4 drying cycles for TRT 1 and 3 drying cycles for TRT 2. Plants were sampled at predawn and at noon, rewatered to runoff at 6 pm and sampled again the next day. A second sampling was made after another 12 days of drying cycles on September 9 and 10, 1990. Five days before the second sampling date, 10 plants (5 per clone) that had been watered daily (from the extra plants) were included in the study and were not watered for 5 days (TRT 0). They were then sampled before and after rewatering. These plants were included to measure the effect of a 5 day stress on unconditioned plants. The last cycle for TRT 1 and TRT 2 plants was 5 and 4 days long, respectively. However, most plants were not well stressed during this period due to cloudy days and cooler weather. Also, since some of these plants were stressed more than others, all plants were rewatered 2 days after this last sampling and then all plants (except control) stressed severely for 10 days until the third sampling date (October 5 to 9, 1990).

On each sampling date, predawn Ψ_w and leaf osmotic potential (Ψ_s) and solar noon net photosynthetic rate, stomatal conductance, and transpiration rate were measured. On the first sampling date before rewatering, water potential at noon was also measured. Predawn Ψ_s of all plants (total 30) was measured on LPI 9 and 10 leaves. Predawn Ψ_s was measured with a thermocouple psychrometer (Decagon Devices Inc., Pullman, WA) on frozen, thawed leaf tissue (Gebre 1989). No correction

was made for a possible dilution by apoplastic water. Osmotic adjustment was based on comparing osmotic potential values of stressed and nonstressed plants. Leaf water potential was measured with a pressure chamber (Ritchie and Hinckley 1975, Turner 1981).

Net photosynthetic rate (μmol m^{-2} s^{-1}), transpiration rate (mmol m^{-2} s^{-1}), and stomatal conductance (mol m^{-2} s^{-1}) were measured on LPI 8 leaves using an ADC LCA–3 open photosynthesis system (Analytical Development Co., London). Each measurement was made under controlled light, humidity, and CO_2 concentration. Uniform light was achieved by moving plants to a growth chamber and taking measurements at about 1100 μmol m^{-2} s^{-1} (wavelengths 400 to 700 nm) of artificial light. The light sensor was calibrated with LI–190SZ (LI–COR, Lincoln, NE) quantum sensor under the growth chamber light. Relative humidity was calibrated with an aspirated hygrometer (Casella and Co. LTD, London). The humidity of incoming air to the leaf chamber was maintained within a range of about 10% on a particular sampling date by using either a desiccator or humidifier on the instrument. CO_2 concentration was maintained between 335 and 350 ppm by volume with a soda lime. Heat build up was reduced by using a fan in the chamber. The environmental conditions during each sampling are shown in Table 1.

A broad leaf chamber (PLC–3(B)) with a leaf area of 6.25 cm^2 was used for photosynthesis measurements. Boundary layer resistance was set at 0.3 m^2 s mol^{-1} according to the ADC LCA–3 manual. Readings were taken when the humidity in the chamber and leaf conductance were stabilized. We found it necessary to check the

Table 1. Leaf chamber conditions on each sampling date. Values are means and standard errors of means of all plants at each measurement.

	Sampling date (1990)								
Variable	Sep 9	Sep 10	Sep 22	Sep 23	Oct 5	Oct 6	Oct 7	Oct 8	Oct 9
Air Temp (°C)	30.2	30.3	30.6	30.9	30.5	30.9	30.9	30.4	30.2
	0.06	0.07	0.07	0.10	0.11	0.14	0.15	0.15	0.16
CO_2 (ppm)	345	342	345	345	344	344	344	344	344
	0.44	0.56	0.28	0.35	0.56	0.48	0.60	0.52	0.48
RH (%)	43	44	34	31	48	37	28	31	24
	0.30	0.38	0.30	0.33	0.47	0.33	0.37	0.61	0.29
PAR (μmol m^{-2} s^{-1})	1108	1120	1133	1135	1129	1130	1138	1147	1142
	3.09	5.46	3.78	4.25	7.20	5.89	8.55	9.77	9.17

stability of conductance because, despite a stable humidity reading, internal CO_2 sometimes was very high resulting in erroneous recordings. Measurement generally took 1 to 2 minutes, though more time (up to 3 min) was needed for equilibrium when plants were sampled on cloudy days (the last three sampling dates Oct 7, 8, and 9, 1990).

Plants were arranged on a greenhouse bench in a randomized complete block design. The blocking criterion was location on the bench. Measurements were completed block by block so that effect due to time was confounded with location. There were five blocks (replications). Within each block, there were six plants (2 clones, 3 stress treatments) for a total of 30 plants in the first sampling period. For the other sampling periods there were 8 plants per block.

The data were analyzed using analysis of variance. Since the block effect was not significant, the data were analyzed as a completely randomized design.

RESULTS

Table 2 shows Ψ_w and Ψ_s of plants at each sampling period. Predawn Ψ_w after rewatering was generally greater than –0.05 MPa and therefore is not included. Figure 1 shows stomatal conductance and net photosynthetic rate during the first period. There were no significant differences between the control and TRT 1 in all variables measured except Ψ_w at noon for Platte. The lowest predawn Ψ_w observed was –0.55 MPa. Despite the high predawn Ψ_w readings, some upper leaves wilted on some of the stressed plants. There were significant differences in all variables between control

Table 2. Water (Ψ_w) and osmotic potentials (Ψ_s) for two eastern cottonwood clones (Ohio Red and Platte) during three sampling periods. Values with different letters in a column and asterisks (*) in a row within a sampling date are significantly different at $\alpha \leq 0.05$.

	September 9 (before watering)						September 10 (after watering)	
	Predawn Ψ_w		Predawn Ψ_s		Noon Ψ_w		Predawn Ψ_s	
Treatment	Ohio	Platte	Ohio	Platte	Ohio	Platte	Ohio	Platte
Control	–0.05a	–0.03a	–1.51a	–1.47a	–0.86a	–0.83a	–1.55a	–1.52a
TRT 1	–0.05a	–0.04a	–1.63a	–1.55a	–0.96a	–0.64b	–1.59a	–1.48a
TRT 2	–0.32b	–0.21b	–1.79b	–1.70b	–1.23a	–1.09c	–1.68a	–1.70b

	September 22 (before watering)				September 23 (after watering)	
	Predawn Ψ_w		Predawn Ψ_s		Predawn Ψ_s	
Treatment	Ohio	Platte	Ohio	Platte	Ohio	Platte
Control	–0.06a	–0.03a	–1.55a	–1.48a	–1.60a	–1.52a
TRT 0	–0.09a	–0.09b	–1.63ab	–1.51a	–1.59a	–1.48a
TRT 1	–0.19a*	–0.08ab*	–1.72ab	–1.52a	–1.64a	–1.61a
TRT 2	–0.48b*	–0.10b*	–1.77b*	–1.56a*	–1.78b*	–1.60a*

	October 5 (before watering)				October 6 (after watering)	
	Predawn Ψ_w		Predawn Ψ_s		Predawn Ψ_s	
Treatment	Ohio	Platte	Ohio	Platte	Ohio	Platte
Control	–0.08a*	–0.05a*	–1.65a*	–1.52a*	–1.57a*	–1.48a*
TRT 0	–0.88b	–0.45b	–1.80ab	–1.67ab	–1.60a	–1.54ab
TRT 1	–1.16b	–0.84c	–1.95ab	–1.81b	–1.67a*	–1.49ab*
TRT 2	–1.23b	–1.05c	–1.88b	–1.78b	–1.64a*	–1.38b*

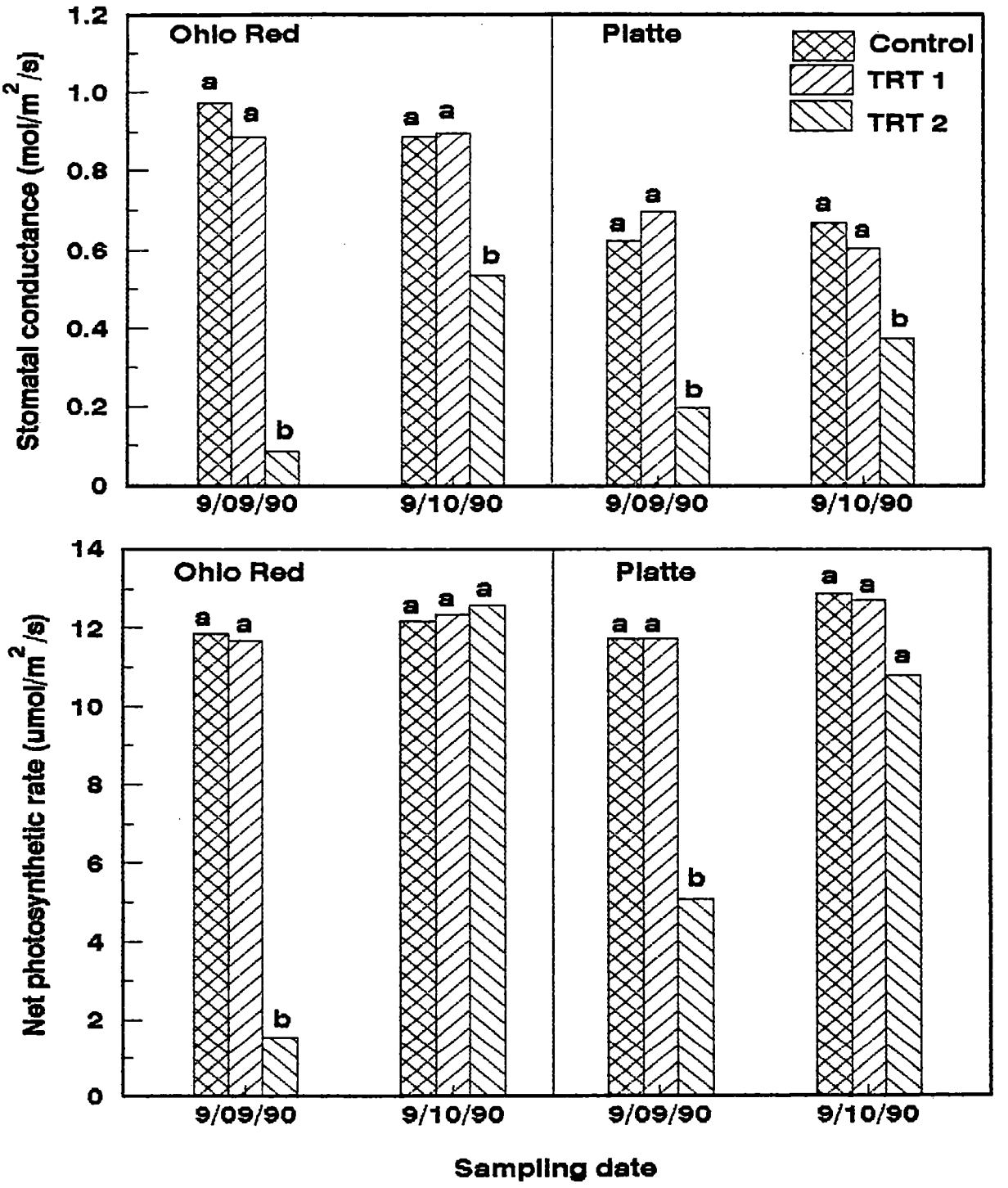

Fig. 1. Stomatal conductance and net photosynthetic rate of two eastern cottonwood clones before (9/9/90) and 18 h after rewatering (9/10/90) (n=5). Values with the same letters on a sampling date were not significantly different (P = 0.05).

and TRT 2 before plants were rewatered (September 9). Clones were not significantly different from each other in any of the variables measured on September 9.

After rewatering and overnight recovery, photosynthesis of Ohio Red was slightly higher in TRT 2 plants than control. There was no significant difference in predawn Ψ_s between control and TRT 2 for Ohio Red. Hence, there was no osmotic adjustment. Platte on the other hand showed a significant difference, an osmotic adjustment of –0.18 MPa in TRT 2 plants. There was no significant difference in photosynthesis in either clone, while stomatal conductance was significantly lower in the control and TRT 1 than TRT 2 plants. Ohio Red had significantly higher stomatal conductance than Platte in the control and TRT 1 but not TRT 2 plants.

Stomatal conductance and net photosynthetic rate for the second period (September 22–23) are shown in Figure 2. There were no significant differences among treatments in all variables for Platte. Ohio Red TRT 2 plants had significantly lower values than control in all variables measured. Ohio Red plants in TRT 2 had significantly lower stomatal conductance, photosynthetic rate, and predawn Ψ_w than Platte (Table 2, Figure 2).

After rewatering, TRT 2 plants of Ohio Red had significantly lower stomatal conductance and Ψ_s than other treatments, and showed an osmotic adjustment of –0.18 MPa. Stomatal conductance of Platte in TRT 1 and 2 was significantly lower than the control. There was no difference between treatments in predawn Ψ_s in Platte (Table 2, Figure 2).

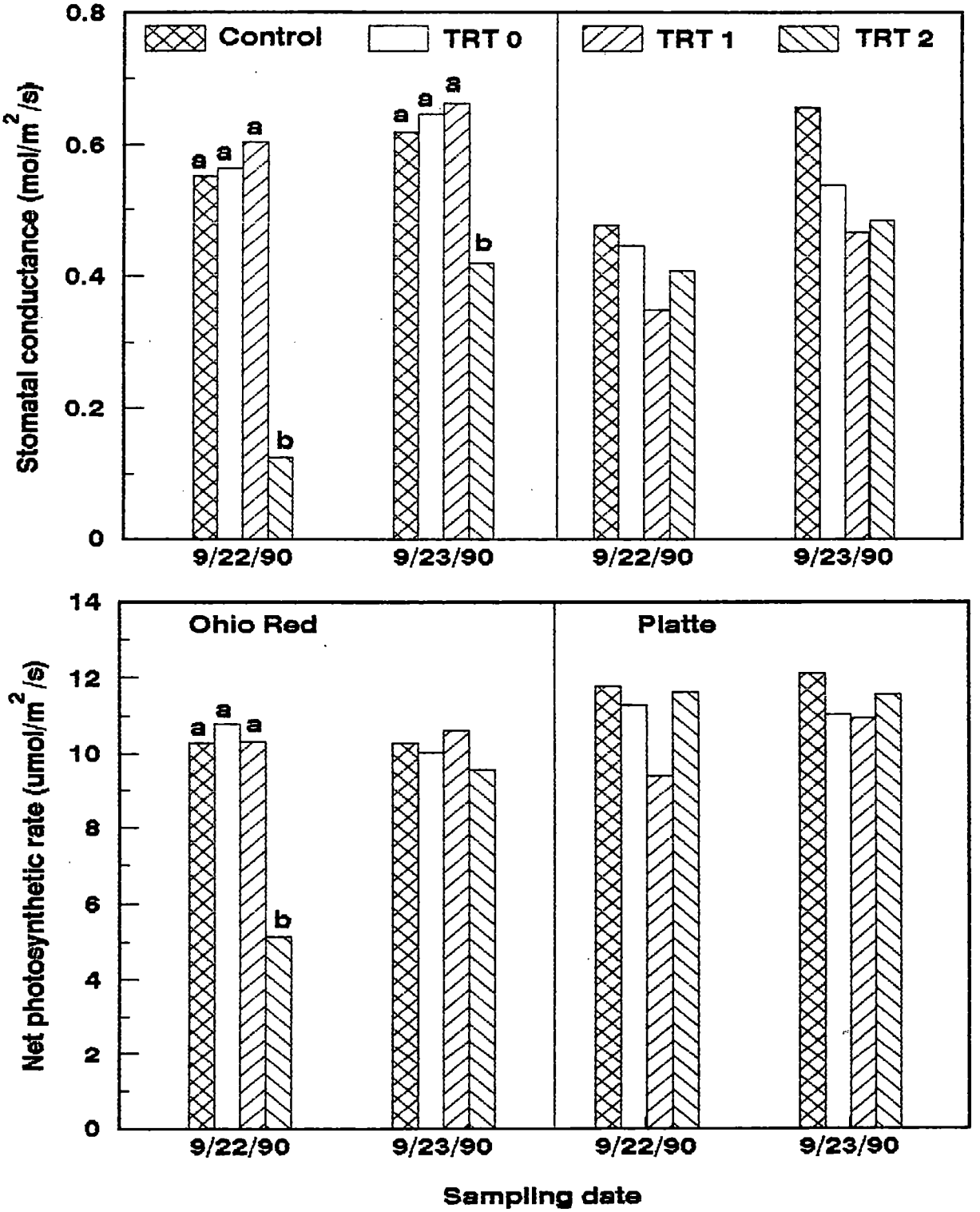

Fig. 2. Stomatal conductance and net photosynthetic rate of two eastern cottonwood clones before (9/22/90) and 18 h after rewatering (9/23/90) (n=5). Values with the same or no letters on a sampling date were not significantly different (P = 0.05).

Figures 3 and 4 show the net photosynthetic rate and stomatal conductance, respectively, before recovery and during recovery for the third period. Most plants in TRT 1 and 2 were respiring and had closed stomata as indicated by negative photosynthesis values and near zero stomatal conductance on October 5, 1990. The minimum predawn water potential reached during this stress period was –3.1 MPa. Four plants with predawn water potential ranging from –1.90 to –3.1 MPa did not recover when rehydrated, though the plants produced new leaves later. Three plants (1 Ohio Red and 1 Platte from TRT 2, and 1 Platte from TRT 1) were not included in the final analysis because they were not as severely stressed as the other plants in their groups (their predawn Ψ_w was greater than –0.5 MPa). There was little change in significant differences, however, whether these plants were included or removed. On October 5, there were significant differences in all variables for both clones between the control and other treatments. There were no significant differences between clones in all treatments except the control. In the control, Ohio Red plants had higher stomatal conductance, and lower predawn Ψ_w and Ψ_s (Figure 4, Table 2).

On the first day of rewatering, photosynthesis and stomatal conductance of stressed plants did not recover fully and were significantly lower than nonstressed control plants. There were no differences in predawn Ψ_s, indicating no osmotic adjustment. There were significant differences between clones in Ψ_s and stomatal conductance except in TRT 0 plants (Table 2).

On the second day of rewatering, stomatal conductance of control plants was higher than stressed plants. Photosynthesis for Platte was significantly lower than for

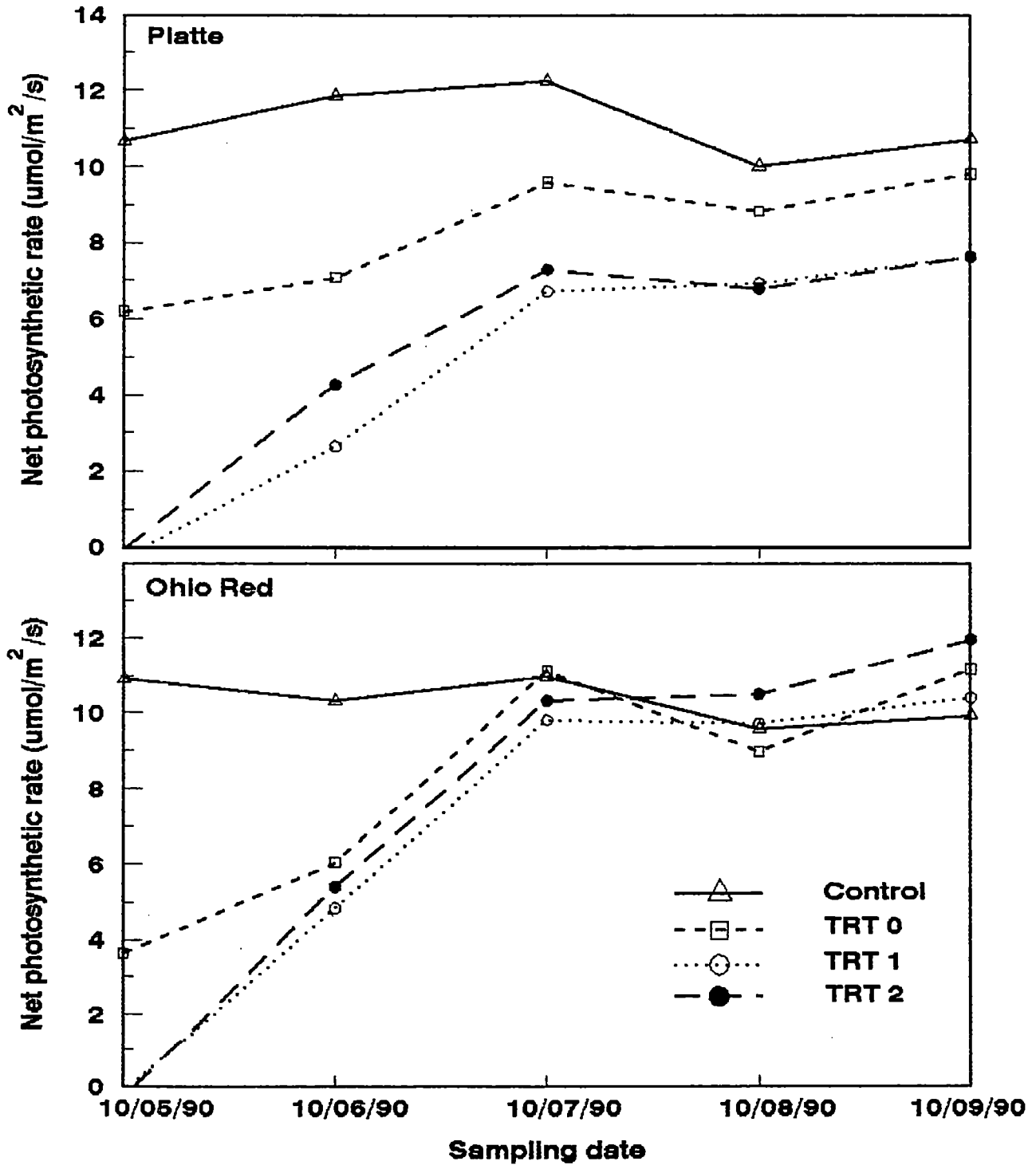

Fig. 3. Net photosynthetic rate of two eastern cottonwood clones before (10/05/90) and 18 h after rewatering (10/06/-10/09/90). Each point is a mean of 5 plants except n=3 in TRT 2, n=4 for Ohio Red in TRT 0.

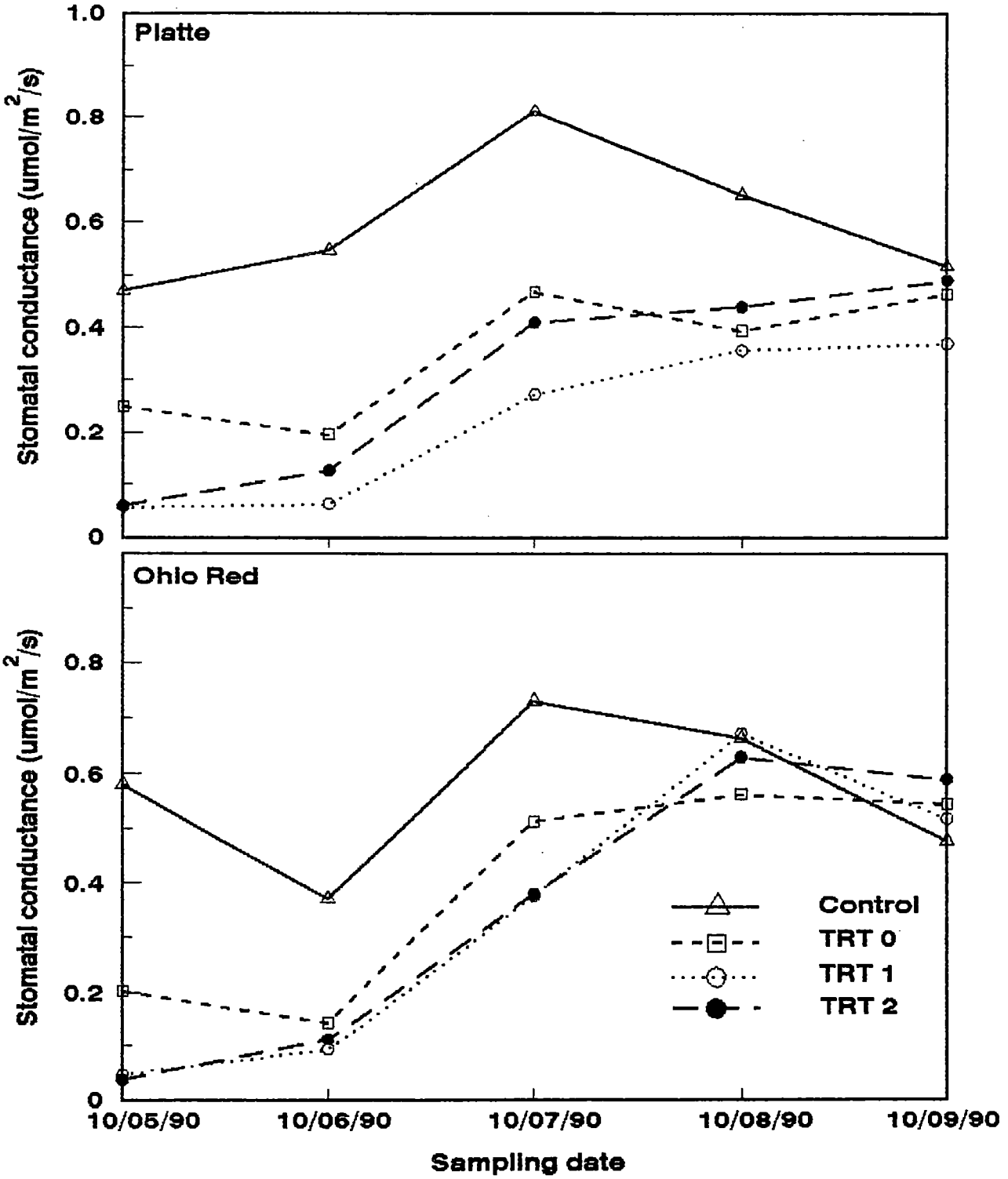

Fig. 4. Stomatal conductance of two eastern cottonwood clones before (10/05/90) and 18 h after rewatering (10/06/-10/09/90). Each point is a mean of 5 plants except n=3 in TRT 2, n=4 for Ohio Red in TRT 0.

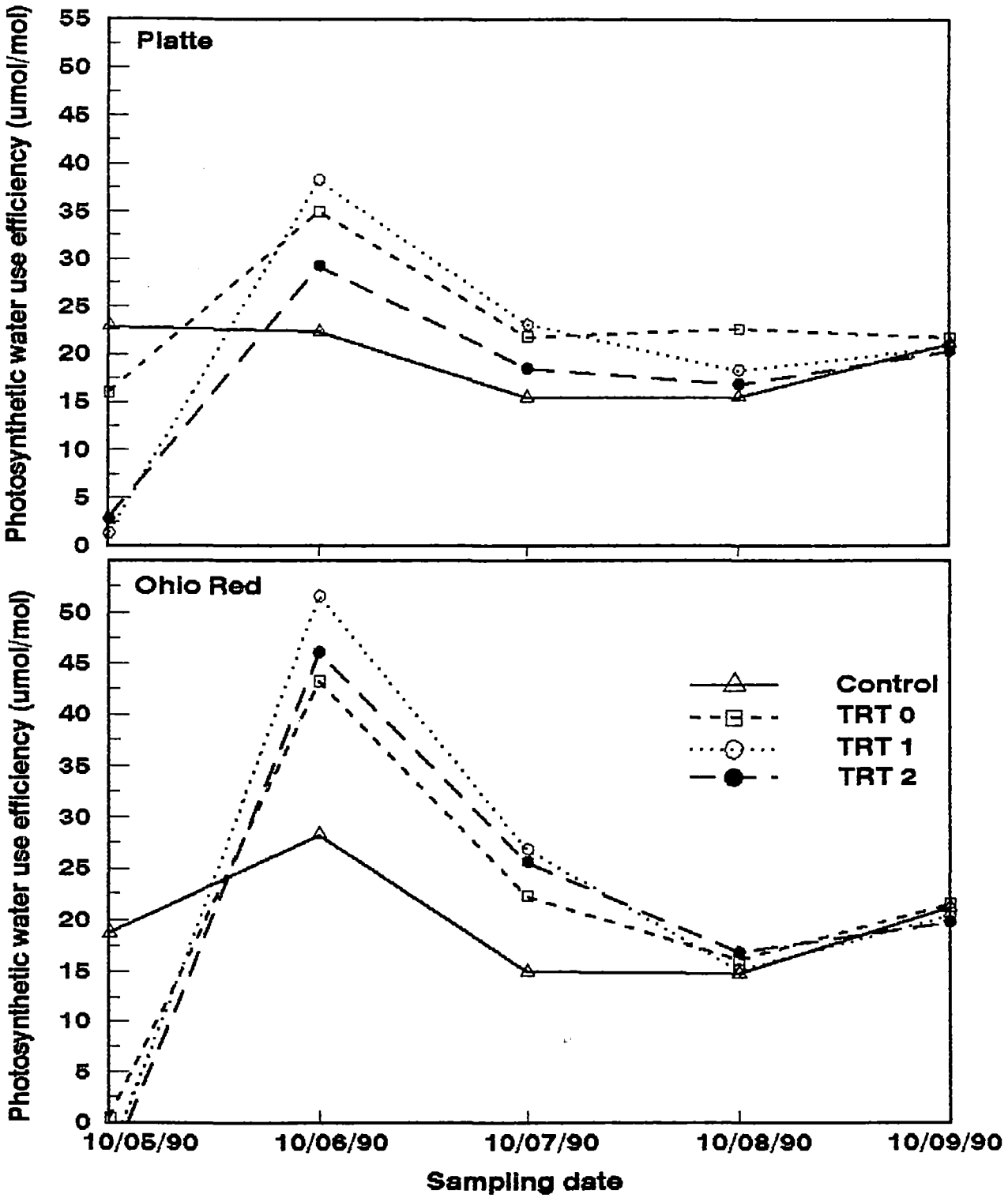

Fig. 5. Photosynthetic water use efficiency (umol/mol) for two eastern cottonwood clones before (10/05/90) and after rewatering (10/06-10/09/90).

Ohio Red during the recovery period in TRT 1 plants. There were no other significant differences among treatments and between clones for the remaining recovery period, though nonstressed Ohio Red plants had lower (nonsignificant) photosynthetic rates than Platte. In stressed plants however, Ohio Red had mostly higher (nonsignificant) photosynthetic rates than Platte.

Figure 5 shows photosynthetic water use efficiency (a ratio of net photosynthetic rate to stomatal conductance) for the last sampling period. There were significant differences between control and stressed plants on the first two days of rewatering.

DISCUSSION

A small amount of osmotic adjustment occurred in both clones at different periods. This may have been due to the difference in the degree of stress of each clone experienced, though watering was withheld for an equal number of days. No osmotic adjustment was observed at severe stress, possibly because plants were using accumulated solutes for respiration. It is also possible that any effect of the preconditioning treatment on solute accumulation was lost when plants were rewatered twice at the end of the second period (Turner and Jones 1980). In a previous field study, we found that Ohio Red typically had higher predawn Ψ_s than Platte. However, in the present study, whenever differences existed, Ohio Red had lower Ψ_s than Platte. Pallardy and Kozlowski (1980) had reported that field–grown Populus plants have thicker cuticle and waxy surfaces than those grown in a controlled environment. From

our observation, the greenhouse–grown plants were more succulent than field–grown plants. From dry weight fraction measurements (leaf dry weight:turgid weight ratio) taken on October 6, 1990 (rewatered plants) lower, nonsignificant, values were observed for Platte (0.25) than for Ohio Red (0.29)(data not shown). The values for Platte (but not for Ohio Red) were also lower in the these greenhouse–grown plants than the field–grown plants (0.30)(Gebre 1989) indicating succulence was more common on Platte. Since Ψ_s values were not corrected for a possible dilution by apoplastic water (in both studies), the difference in leaf structures may have contributed to difference in dilution error. This assumes however, there was a difference in apoplastic water between greenhouse– and field–grown plants. It also assumes that there were differences in apoplastic water between the two clones. Coleman (1982) found that Ohio Red had significantly higher bound water fraction than Platte in an outdoor shadehouse–grown plants. Wenkert (1980) reported that Ψ_s of greenhouse– and field–grown corn (Zea mays L.) plants were 11% and 16% more dilute than Ψ_s measured by the pressure–volume method, respectively.

Early in August, we observed upper leaves wilting at high predawn Ψ_w. In October, however, leaves seemed healthy and showed no sign of wilting until a day before sampling. Some of the factors for these differences may be cooler weather and better established root systems (more than 5 months old) in October. Water loss in August due to higher temperatures may have exceeded the rate of water uptake by the younger root systems.

Both clones closed their stomata during the severe stress period. There was no benefit from the drying cycles as stomatal conductances and net photosynthetic rates for TRT 0 were not significantly different form the prestressed treatments (TRT 1 and TRT 2). Kelliher and Tauer (1980) found that dry site eastern cottonwood clones had less sensitive stomata than wet site clones even under well watered conditions, and suggested that this trait made these plants more drought tolerant. In our study, Platte had mostly lower stomatal conductance than Ohio Red in control plants. But this relationship was not consistent in stressed plants, possibly due to differences in the level of stress between the two clones.

Recovery to control levels was immediate upon rewatering in the first two sampling periods. After the severe stress in the third sampling period, however, recovery was slow, despite full recovery in predawn Ψ_w. Ohio Red plants recovered by day 2 of rehydration while Platte did not recover even by day 4 of rehydration. Regehr et al. (1975) reported complete recovery of photosynthetic rate of a P. deltoides provenance from Minnesota 36 hours after recovery from a leaf water potential of –1.05 MPa, while 46 hours were necessary to reach 50% of maximum photosynthesis when leaf water potential had dropped to –1.55 MPa. The average minimum predawn water potential of stressed plants during the last stress period of our study was –1.23 MPa and the first recovery measurement was 18 h after rewatering. Ohio Red had higher photosynthetic rates though not significantly different for recovered stressed plants than for control plants. This was despite the fact that

conductance values in the stressed plants were lower than in the control plants. This pattern was observed on the first and third sampling periods in Ohio Red only.

Ceulemans et al. (1983) reported an increase in photosynthetic rate after rehydration of stressed Hevea brasiliensis (Muell. Agr.) plants. Similar patterns were reported by Ludlow (1975) in Panicum maximum var. trichoglume. Ceulemans et al. (1983) suggested that this type of increase may be due to increased root activity after plants are rewatered. Ludlow (1975) proposed two hypotheses: 1) stress–induced enhancement of photosynthetic capacity and 2) ageing effect, i.e. stressed leaves may be physiologically younger than leaves with the same chronological age. This assumes that water stress suspends ageing, and means that our LPI 8 leaves of control plants would be physiologically younger than LPI 8 leaves of stressed plants. This also would be more apparent in Platte than Ohio Red, because Platte grows at a faster rate than Ohio Red (Coleman 1982, Gebre 1989). However, the increased photosynthetic rate after rewatering of stressed plants was observed only in Ohio Red. Based on the observation that the increased photosynthetic rate upon rewatering was similar among stressed leaves, Ludlow (1975) suggested that the increase was independent of the duration and intensity of stress and age. We also found no significant differences among stressed treatments but recovery was dependent on the intensity of stress, i.e. recovery was immediate after a mild stress period (Sept 9, 10 data) while it was delayed on severely stressed plants (Figure 1, 3).

Since the increase we observed in photosynthetic rate after stress was not directly related to the same degree of increase in stomatal conductance, other

changes either in the chloroplast or CO^2 use efficiency may be involved. Havaux et al. (1988) showed that there was variation among poplar clones in tolerance of the photochemical apparatus of chloroplasts to water stress among poplar clones. Matthews and Boyer (1984) reported that photosynthesis at low water potentials was limited more by loss of chloroplast activity than by reduced stomatal conductance in sunflower (Helianthus annuus L.). In severely desiccated sunflower leaves (–1.7 MPa), Boyer (1971) found a complete recovery of chloroplast photochemical activity after rewatering while recovery of photosynthesis and stomatal conductance was slow. This was despite a complete recovery in leaf water potential.

Davies and Kozlowski (1977) calculated photosynthetic water use efficiency (PWUE) of five woody species. They found that those species from dry sites had higher efficiencies than those from moist sites and that maximum stomatal opening was not obtained in dry site species for four days following rewatering. They concluded that plants with high PWUE at high water stress levels, and/or delayed stomatal opening following rewatering after drought, might compete better on drier sites. Our plants when severely stressed generally showed no photosynthesis. On the first day of rewatering, however, Ohio Red had higher PWUE than Platte. In both clones, PWUE was greater in stressed than control plants (Figure 5). Differences in PWUE disappeared after the third and fourth day of rewatering for Ohio Red and Platte, respectively. The slow recovery in the net photosynthetic rate of Platte seemed related to the slow recovery of stomatal conductance as can be seen from the low PWUE. That is, both photosynthetic rates and stomatal conductance values remained

low in stressed plants. For Ohio Red plants, recovery of photosynthetic rates was faster than recovery of stomatal conductance. These differences between clones may indicate different drought adaptation mechanisms or there may have been some damage to the photosynthetic system of Platte. The latter is however unlikely in this study, because lower photosynthetic rates (nonsignificant) were also observed during the recovery of stressed plants from a predawn Ψ_w of only –0.2 MPa (first period) corresponding to a lower stomatal conductance.

In conclusion, osmotic adjustment was limited to less than –0.2 MPa in both clones and was not observed after a severe water stress. Based on the slow recovery of stomatal conductance, both clones may compete well under moderate water stress. As long as leaves were not killed, photosynthetic rates of Ohio Red were higher after a prestress treatment. This however was not related to osmotic adjustment. Because of its rapid recovery and increased photosynthetic rate after a stress period, total productivity of Ohio Red may be less affected by short stress periods than that of Platte.

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